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THE RELATIONSHIPS OF OLD AND NEW WORLD MELANIANS

By J. P. E. Morrison

Recent anatomical observations on the reproductive systems of certain so-called "melanian" fresh-water snails and their marine relatives have clarified to a remarkable degree the supergeneric relationships of these fresh-water forms.

The family of Melanians, in the broad sense, is a biological absurdity. We have the anomaly of one fresh-water "family" of snails derived from or at least structurally identical in peculiar animal characters to and ancestrally related to three separate and distinct marine families. On the other hand, the biological picture has been previously misunderstood largely because of the concurrent and convergent evolution of the three fresh-water groups, Pleuroceridae, Melanopsidae, and Thiaridae, from ancestors common to the marine families Cerithiidae, Modulidae, and Planaxidae, respectively.

The family Melanopsidae is definitely known living only in Europe. At present, the exact placement of the genus *Zemelanopsis* living in fresh waters of New Zealand is uncertain, since its reproductive characters are as yet unknown. In spite of obvious differences in shape, the shells of the marine genus *Modulus* possess at least a well-indicated columellar notch of the aperture, to corroborate the biological relationship indicated by the almost identical female egg-laying structure in the right side of the foot of *Modulus* and *Melanopsis*.

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The family Pleuroceridae, fresh-water representative of the ancestral cerithiid stock, is now known to include species living in Africa, Asia, and the Americas.

The family Thiaridae, likewise, is known from Africa, Asia, and America. With identical reproductive characters, the Thiaridae are only too obviously the fresh-water relatives of the Planaxidae. It is only when the Melanopsidae, Pleuroceridae, and Thiaridae are separated that their zoogeographic story can be read without confusion. Perfect separation of these three fresh-water families can only be accomplished by reference to characters of the animals, particularly the reproductive characters. Radular, opercular, or shell characters that will completely separate these families are nonexistent because of their concurrent and convergent evolution.

The following key to the major groups of the Melanian complex is given here as the most logical one possible. In the author's opinion, it represents the true biological relationship of these groups.

a.[1] Reproduction dioecious; males present in species.
  b.[1] Female with large grooved "ovipositor" in pit on right side of foot; few eggs of proportionately large size.
    c.[1] Marine shells ..... **Modulidae**
    c.[2] Fresh-water shells ..... **Melanopsidae**
  b.[2] Female with egg-laying sinus and rudimentary papilla, or no special structure on right side of foot; numerous eggs of proportionately smaller size.
    d.[1] Marine shells ..... **Cerithiidae**
    d.[2] Fresh-water shells ..... **Pleuroceridae**
      e.[1] Males with no intromittent structures.
        f.[1] Females oviparous, with egg-laying sinus in right side of foot. **Pleurocerinae**
        f.[2] Females ovoviviparous, without egg-laying sinus; brood pouch uterine, the enlarged end of the oviduct ..... **Lavigeriinae**
      e.[2] Males with eversible "penis" in mantle edge near end of vas deferens; females ovoviviparous; brood pouch uterine ..... **Tiphobiinae**
a.[2] Reproduction parthenogenetic; no males present in species; brood pouch not uterine, but adventitious (subhaemocoelic) in the neck region, with opening on right side of neck.
  g.[1] Marine shells ..... **Planaxidae**
  g.[2] Fresh-water shells ..... **Thiaridae**

Family Melanopsidae (Europe)

Two genera from the fresh waters of Europe have been studied and proven to belong to the family *Melanopsidae*. They are more specialized than the Asiatic and American Pleuroceridae, possessing a much larger "ovipositor" and laying a much smaller number of proportionately much larger eggs.

According to studies by Ankel (1928), *Fagotia esperi* (Ferussac) has the same reproductive anatomy of the female as does *Melanopsis*. The few large eggs (1 mm. in size) are laid singly in an irregular capsule.

Melanopsis dufourii (Ferussac) from Elche, Alicante Province, Spain, has been examined by me. Unlike the animals of the North American Pleuroceridae, in this species at least, the smooth mantle edge is continuous beneath the back of the foot, forming a circle around the aperture. In the female the end of the oviduct is quite far behind the mantle edge and simple, as is typical for the group. The egg-laying groove is not long, and does not even reach the mantle edge. The pit is enormously developed and has a large, whitish, tongue-shaped, basally-attached "ovipositor," with a groove on its posterior dorsal face, toward the rest of the pit. According to Ankel (1928), a few proportionately large eggs are laid by *Melanopsis*.

Family Pleuroceridae (in the Americas)

Subfamily pleurocerinae

All known American members of Pleuroceridae are oviparous, including those from North, Central, and South America and the West Indies. In other words, every American genus and species for which the characters of reproduction are known is egg-laying, with an egg-laying sinus or pit in the right side of the foot of the females. The presence of this pit is the single morphological character that proves them to belong to the typical subfamily. There is every indication that all the American genera and species of Pleuroceridae belong here, although some of the North American genera are still unrecorded as to critical animal characters.

Subfamily pleurocerinae (in North America)

Genus *Oxytrema* Rafinesque, 1819

Oxytrema Rafinesque is the earliest and correct name for one of the most widespread "Melanian" genera in the world. This genus includes numerous North American species whose ranges extend from the Atlantic to the Pacific coasts and from southern Canada to Florida and Texas. It also includes North American fossils, as well as a number of Recent species from southeast Asia (Korea, China, and Thailand). All the species called *"Pleurocera"* by Bryant Walker, and other authors who followed him blindly, and all the species called *"Goniobasis"* (with very few exceptions) belong to this genus. Their eggs are laid in a single row in a close, irregularly spiral group, in apparent flat clusters of 3 to 10 egg capsules in each small egg mass, the whole covered with sand grains as recorded by Van Cleave (1932), Winsor (1933), and Woodward (1934).

Rafinesque originally described *Oxytrema* (1819, p. 423), including young specimens of both his genus *Pleurocera* and this one. There were no specific names included. Blainville, in 1824 and again in 1825 (p. 442), placed one species of Rafinesque under this generic name. He gave as the sole example of the subgenus *Pleurocerus* (*Oxytrema*) *acutus* (Rafinesque), validating the specific name in 1824. Rafinesque (1831, p. 3) again described his *Pleurocera acuta*, and at the same time declared he had given the name in 1818. From 1824 on, *Oxytrema* has been the earliest available name for the group because the genotype was fixed at that time as *Pleurocera* (*Oxytrema*) *acuta* Blainville by monotypy. With no serious question ever raised about the identity of *acuta*, the genotype, doubts about the identity of the genus *Oxytrema* vanish.

The eastern American (Appalachian) species of *Oxytrema* include some whose shells are almost completely smooth as adults, such as *O. symmetrica* (Haldeman); some with spiral sculpture predominant, such as *O. virginica multilineata* (Say); others with axial sculpture strong, such as *O. laqueata* (Say); and still others with both axial and spiral lirae to produce reticulate or nodose sculpture, such as *O. catenaria* (Say).

In exactly parallel fashion, as should be expected of congeneric stocks, the western American species now known to belong to *Oxytrema* show the same rather complete range of sculpture from smooth to axially and spirally sculptured adult shells. The easternmost living representative of the Rocky Mountain group of species is *O. comalensis* (Pilsbry). This species from Texas belongs to this minor group within the genus, possessing the same minutae of female reproductive characters as does *O. plicifera* (Lea) from Oregon and Washington. Most if not all the western America Tertiary fossil species described as "*Melania*," "*Goniobasis*," and "*Pachychilus*," from Texas to Washington, were members of this genus *Oxytrema* Rafinesque. For example, "*Ambloxus*" *olequaensis* Arnold and Hannibal (Hannibal, 1912, p. 178, pl. 8, fig. 27) closely resembles the smoother phase of the living *Oxytrema silicula* (Gould) from the same region, while "*Pachychilus*" *drakei* Arnold and Hannibal (Hannibal, 1912, p. 183, pl. 8, fig. 26) is close to the living species *Oxytrema plicifera* (Lea). Certain other fossil species from the Rocky Mountain region parallel eastern forms in the possession of cancellate or reticulate sculpture. Species known from the fossil record indicate the previous continuity of geographic distribution from Washington to Texas, now noncontinuous since much of the intervening area (progressively desiccated since the Miocene) is now unsuited to survival of pleurocerine freshwater snails.

Female animals of *Oxytrema canaliculatum undulatum* (Say) from

the Kentucky River, of *Oxytrema deshayesiana* (Lea) from the Tennessee River, of *Oxytrema bulbosa* (Gould) from eastern Oregon, and of *Oxytrema nodifila* (Martens) from the Han River, Korea, have been examined by me and sketched to show the egg-laying groove and the "ovipositor" pit on the right side of the foot (see pl. 11).

Section *Strephobasis* Lea, 1861

The group named *Strephobasis* by Lea (1861, p. 96), with the genotype *Oxytrema* (*Strephobasis*) *plena* Anthony, as stated by Pilsbry (1896a, p. 496), is only an extreme section of the genus, according to shell characters. This small group, which is confined to the larger rivers of the upper Tennessee drainage, is exactly parallel to *Goniobasis*, sensu stricto, from the Coosa River drainage. The animal characters must be examined to determine whether this group is identical to or biologically distinct from *Oxytrema*, sensu stricto, and *Goniobasis*, sensu stricto.

Genus *Gyrotoma* Shuttleworth, 1845

Gyrotoma Shuttleworth (1845, p. 88), based on the genotype (*Gyrotoma ovoideum* Shuttleworth=) *Gyrotoma excisum* (Lea), is confined to the Coosa River drainage. As Goodrich (1924, p. 6) has hinted, the group named *Goniobasis* by Lea in 1862 (genotype by subsequent designation by Hannibal 1912: *G. osculata* Lea) may eventually prove to be most closely related to *Gyrotoma*. It is possible that *Goniobasis*, sensu stricto, may be a subgenus of *Gyrotoma* different only by lack of or development of the fissure in the lip. Study of the animal characters (as yet unknown) of the genotype must prove the true biological position of *Goniobasis*.

Genus *Mudalia* Haldeman, 1840

Mudalia of Haldeman, whose genotype is *Mudalia carinata* (Bruguière) from the Atlantic coastal region, includes *trilineata* (Say) of the Ohio River and the more widespread "*Goniobasis*" *livescens* (Menke) from the upper St. Lawrence River and upper Mississippi River areas. The single carina typical of adolescent shells and the egg-laying habits are identical in *carinata* (Winsor, 1933) and in *livescens* (Jewell, 1931). Figures 10 and 14 of Goodrich (1945, pl. 1) show how closely the shape of adult shells of *livescens* may vary toward the usual shape of adult shells of *carinata*. The eggs of *Mudalia* are laid singly; that is, there is only one egg capsule in each egg mass.

Genus *Leptoxis* Rafinesque, 1819

Leptoxis of Rafinesque is the earliest name available for the American species related to the genotype *L. praerosa* (Say), and must be so used. Pilsbry (1917, p. 113) has stated the case for priority of *Lep-*

toxis Rafinesque 1819 over *Anculosa* Say 1821 so clearly that Walker's 1918 refusal to follow this needed correction of nomenclature appears at present to be only a prejudiced personal objection to the change. As in other similar cases, most American authors, especially those concerned with biology rather than nomenclature, from 1918 to date have followed Walker not because they had critically checked the generic names used by him, but simply because it was the most recent comprehensive classification outline for North American fresh-water shells. As stated elsewhere, this incorrect usage following Walker dates only from Walker, and has only 33 years standing, which is not enough to even raise any questions of usage over priority of names.

For the record Chenu states (Haldeman, 1847–1848, p. 1, footnote) that he and not Haldeman put the name *Leptoxis* of Rafinesque on Haldeman's pictorial monograph of the genus. Thus Chenu, and Pilsbry by formally designating *praerosa* as genotype in 1917, completely cleared up all doubts, concerning Rafinesque's genus, which had existed prior to 1848.

Genus *Eurycaelon* Lea, 1864

Eurycaelon of Lea (1864, p. 3) has as genotype *Eurycaelon anthonyi* (Redfield) by subsequent designation by Walker (1918, p. 36). The two known species, *Eurycaelon crassa* (Haldeman) 1841 and *E. anthonyi* (Redfield) 1854 are confined to the larger rivers of the upper Tennessee drainage as reported by Goodrich (1931). In this connection must be mentioned the fact that the two names *cristata* Anthony (young specimens) and *anthonyi* Redfield (adult specimens) were published simultaneously in April 1854, according to the printed signature dates of volume 6 of the Annals of the Lyceum of Natural History of New York. Goodrich, acting as first reviser, selected *anthonyi* Redfield, on page 130 of volume 6 of the above Annals, over the name *cristata* of Anthony, on page 108, which he placed in synonymy. In this way Goodrich avoided a confusing change of name of the genotype.

Genus *Pleurocera* Rafinesque, 1818

Pleurocera of Rafinesque became monotypic in 1820 with the valid publication by Rafinesque of *Pleurocera verucosa.* Tryon in 1864 and 1873 did not include the genotype in his usage, so his usage was biologically and nomenclatorially wrong. Pilsbry in 1896 questioned the genotype. Hannibal (1912, p. 169) formally designated the monotype species *verrucosa* Rafinesque as the genotype, being followed correctly by Pilsbry in 1917.

Bryant Walker, in his 1918 classification, continued to use Tryon's incorrect name for the genus when he used only the second available

name, *Lithasia* Haldeman (1840), which has the species *geniculata* of Haldeman for genotype.

The smooth species from the Kentucky River named *Ellipstoma zonalis* by Rafinesque in 1818 can only be the species commonly known as *Lithasia obovata* Say 1829. With over 10 years priority, the specific name of Rafinesque must be used. Animals of *Pleurocera zonalis* Rafinesque personally collected from the Kentucky River have been examined and sketched. The female egg-laying characters are illustrated in figure 4 of plate 11.

Subgenus *Ellipstoma* Rafinesque, 1818

In spite of the extreme brevity of Rafinesque's original description (1818b, p. 42), critical reading indicates that this name applies only to the group afterward named *Angitrema* by Haldeman (1841a). Hannibal (1912, p. 168) formally designated Rafinesque's first species, *Ellipstoma gibbosa*, as the genotype, although he misidentified that species. When one approaches the identification of *gibbosa* from every angle it is evident that there is only one kind of snail in the Ohio and Wabash Rivers with "a large knob behind the outward lip." This is the same species named almost three years later as *Melania armigera* Say (1821, p. 178).

Critical examination of the animal characters of the genotype *Pleurocera* (*Ellipstoma*) *gibbosa* Rafinesque is needed to check the biological distinction of *Ellipstoma* as a subgenus, a separate genus, or a synonym of *Pleurocera*, sensu stricto.

Genus *Anaplocamus* Dall, 1895

Anaplocamus of Dall (1895, p. 8), mistakenly described as an Alaskan marine shell because of accidentally transposed locality labels, is a monotypic genus based on the species *"Anculosa" dilatata* Conrad (Rehder, 1942, p. 49). This species of the Kanawha River drainage and the upper Cheat River of the Allegheny drainage is the northern representative of the *Io* group. It has the columellar shell structure of *Io*, not that of *Leptoxis*. From a broad biological viewpoint it may be considered a subgenus of *Io*, or, more conveniently, a separate genus closely related thereto.

Genus *Io* Lea, 1831

The genus *Io* of Lea is well known; it includes the largest living United States Pleuroceridae known. How many species other than the nominal genotype *fluvialis* (Say) there are or were in existence must await studies of the animals to check the magnificent analyses of shells by Adams (1915). Haldeman, in the American edition of

Heck's Iconographic Encyclopaedia (1851, p. 84), has given a general description of the animal of *Io*:

> Its characters and habits are not those of *Fusus*, but of [*Oxytrema*] proper, as distinguished from *Leptoxis;* for although it inhabits the rapids as well as quiet water, in both cases it avoids the current by seeking shelter beneath shelving rocks, or in hollows or crevices in them. The head is large, and with the tentacles much exposed; the foot is as large as in [*Oxytrema*]; the coloration is the same (black lines upon an orange ground); the operculum is subspiral as in [*Oxytrema*], the mantle extends into the canal of the shell, but does not form a closed siphon; the vent is upon the right side; the mouth is a longitudinal slit; the eyes (which are sensitive to the light) are upon a short enlargement of the outer base of the tentacles, which may be a little longer than in [*Oxytrema*], and they are not visibly annulated. It differs from *Fusus*, and resembles [*Oxytrema*] in living upon vegetable food; and it moves along in a sluggish manner, moving the head from side to side upon the bottom. *Io spinosa* and *I. tenebrosa* are merely varieties of *I. fluvialis*. The spinose individuals are much the most abundant, although the species is rare when compared with various species of [*Oxytrema*].

We have taken the liberty of replacing the name "*Melania*" in the foregoing quotation with that of *Oxytrema*, since Haldeman had studied and published as typical of "*Melania*" the animal of *Oxytrema virginica* (Gmelin) (Haldeman, 1841b, p. 21).

In this connection, it must be mentioned that the shells of the group of "*Pleurocera*" *alveare* Conrad (1834, p. 54, pl. 4, fig. 7) look suspiciously like normal sized representatives west of and downstream from the megasomatic *Io*, sensu stricto, species. The generic name *Megara* H. and A. Adams (1854, p. 306) has not hitherto been genotyped. Walker (in litt.), quoted by Goodrich (1928, p. 2, footnote 5), incorrectly reported that Hannibal (1912, pp. 169, 179) had designated the type of *Megara*. Reference to these pages shows that Hannibal listed parts of the original *Megara* twice, with two different species as examples (not as types) in the two synonymy lists 10 pages apart. The genotype here designated is the first species, *Megara alveare* (Conrad) 1834. Animal characters of this group remain a desideratum. If the group is most closely related to *Oxytrema*, as it has usually been regarded, *Megara* will remain as a synonym of *Oxytrema*. If, however, these species should prove upon examination to be closest to *Io* in relationship of animal characters, their group name *Megara* will be available.

Subfamily PLEUROCERINAE (in Central and South America)

Genus *Pachychilus* Lea, 1851

This genus seems to be the ecological replacement of *Oxytrema*, to the southward of the United States. In my opinion, all the known species of this family and subfamily from Central America and the West Indies belong to *Pachychilus*. In this connection, the ichthyol-

ogist S. E. Meek should be given credit as the first known discoverer of the eggs of any member of the family Pleuroceridae. Reporting on collections made in 1906 (Meek, 1908, pp. 205–206), he says:

Sphaeromelania largillierti Phil. This is the largest and by far the most abundant species of shell found in the lake. It is found everywhere along the shore on plants and rocks. This species deposits its eggs in January and February. The eggs are very large and are usually attached to the under side of rocks. This species is so abundant that its large gelatin-like eggs would furnish a considerable amount of food for small fishes. It is a very abundant species in Guatemala and San Salvador to Central Nicaragua.

Goodrich and Van der Schalie (1937, pp. 39, 41, 42) have recorded and described the eggs of three additional species of *Pachychilus* as follows:

Pachychilus glaphyrus (Morelet) 1849. The eggs were found attached to dead leaves, which were abundant in the bottom of the arroyo. The leaves were in only a few inches of water on a mud-silt bottom near shore. The eggs occur in groups of 3 to 5, are round and glassy in appearance, and are irregularly and linearly arranged as a single loosely attached layer. As might be expected in a species as large as *glaphyrus*, the eggs are also large, having a diameter of 3.9 mm. (Arroyo Yalchactila of the Rio de la Pasion, about 4 mi. S. W. of La Ceiba, Alta Vera Paz, Guatemala) . . . .

Pachychilus corvinus (Morelet) 1849. Egg masses of this species were found from which the infant shells were emerging. These were smooth, pinkish carnelian, translucent, and bluntly rounded at the periphery. The whorls varied from 3 to 3½. With growth the shell generally becomes black, even though the adults may be of a mahogany or yellowish color on the body whorls . . . .

Pachychilus pilsbryi Martens 1897. Eggs of this species were found on the lower surfaces of stones in a current near shore. The egg masses occur as flat layers spread out over flat objects. The size of the egg mass varies, the number of eggs in some of them observed running from 8 to 20. The eggs themselves are round, shotlike, and transparent. The whole mass is held together by a gelatinous coating. The average size of the individual eggs is 2.8 mm.

We are indeed fortunate in having on record, in the first four species so known, the egg-laying characters of three subgenera of the genus *Pachychilus*.

Subgenus *Oxymelania* Crosse and Fischer, 1892

Oxymelania Crosse and Fischer (1892, p. 328) possesses the species *schiedianus* Philippi as genotype by original designation. This group of small to medium-sized species has been most completely studied in the San Luis Potosí region by Pilsbry, following the collections made by A. A. Hinkley. In this subgenus, some species of which are widely different in height of spire, and thus of shell outline, the single general identifying character is the possession or prominence of macroscopic spiral lirations on the adult shell. The egg-laying habits for the species *pilsbryi* Martens are quoted above. The synonyms of *Oxymelania* include *Potamanax* Pilsbry (1893, p. 340), named only a few months later, and *Lithasiopsis* Pilsbry (1910, p. 47). In spite of

the great similarity of shells, *Cubaedomus* does not belong here. Animal characters prove it to belong in the family Thiaridae, as recorded below. *Oxymelania* is known to range geographically from the Panuco River system of México to the headwaters of the Usumasinta River in Guatemala.

Subgenus *Pachychilus* Lea, sensu stricto, 1851

Pachychilus Lea (Lea and Lea, 1851, p. 179) originally included only two specific names, *cumingii* Lea and *laevissima* Sowerby. In January 1860, Reeve (1859–1861, pl. 18, fig. 126) designated *laevissima* as the genotype. On the other hand, Reeve's *"laevissima"* was a mixture of the species from Chiapas, México, which has since been mistakenly called *"laevissima"* by many authors, and the true *laevissima* of Sowerby and Lea from La Guayra, Venezuela. Since the mixture of Reeve contained in synonymy the originally included *laevissima* of Sowerby, this designation was valid. Thus the genotype, correctly figured on plate 19, figure 133c, of Reeve (1859–1861) is the only known South American species of the genus. The typical group in Central America is the *corvinus* or *largillierti* group of species, characterized by medium- to large-sized shells with a generally elongate-ovate or elongate-conic outline, rather flat-sided whorls, and almost completely smooth macroscopic sculpture. The egg-laying habits are quoted above. The Cuban species *nigrata* Poey 1858, *fuentesi* Aguayo 1936, and *violaceus* Preston 1911 apparently belong here. Synonyms of *Pachychilus*, sensu stricto, include *Cercimelania* Crosse and Fischer (1892, p. 327) with *P. liebmanni* (Philippi) as genotype, and *Sphaeromelania* Rovereto (1899, p. 109) with the same genotype as *Pachychilus*, since it was proposed as a substitute name. Apparently both Crosse and Fischer and Hannibal did not know of Reeve's type designation and incorrectly listed *P. graphium* (Morelet) as the genotype.

Subgenus *Glyptomelania* Crosse and Fischer, 1892

Glyptomelania Crosse and Fischer (1892, p. 328) is confined to Central America. This group of large shells with variable to nodose or subspinose sculpture includes *glaphyrus* (Morelet), the subgenotype by original designation. The eggs of this species have been recorded by Goodrich and Van der Schalie as quoted above.

Subgenus *Pilsbrychilus* Morrison, 1952

Pilsbrychilus Morrison (1952, p. 7) is distinguished from other known members of the genus by the markedly sinuous lip-margin developed in mature adult shells. It seems probable that examination of the animal will serve to corroborate the distinction of this group now based

solely on shell characters. The genotype by original designation is *Pachychilus* (*Pilsbrychilus*) *dalli* Pilsbry, which was first validly published April 17, 1896, in Science (vol. 3, p. 608) ahead of the complete description by Pilsbry in Proceedings of the Academy of Natural Sciences of Philadelphia, June 16, 1896 (p. 269). Fortunately, this earliest validation preceded the typographical error "*walli*," which appeared in Zoologischer Anzeiger in May 1896.

Genus *Doryssa* H. and A. Adams, 1854

Doryssa H. and A. Adams (1854, p. 304), whose genotype is *D. atra* (Bruguière) from Suriname, ecologically and geographically replaces *Pachychilus* in northern South America from Venezuela to the Guianas and Brazil. In both these genera the females have a well-developed genital groove ending in the characteristic pleurocerine glandular egg-laying sinus near the right edge of the foot. The males lack this groove. *Doryssa consolidata* (Bruguière) was personally collected by the hundreds from rocks in the Mazaruni and Cuyuni Rivers of the Essiquibo system, British Guiana, in the summer of 1925. At that time the shells were cleaned and the radulae (see Baker, 1930, p. 30) extracted from the animals for future study of variation. Although at that time I did not know what characters were critical for subfamily classification, no difference of gross anatomy was observed between this British Guiana *Doryssa* and the North American species *Oxytrema semicarinata* (Say), already critically and completely personally studied near Lexington, Ky., in 1924. The egg-laying season of *Doryssa* is apparently still unrecorded. It was not observed during June, July, or August in the Kartabo region. *Sheppardiconcha* Marshall and Bowles (1932, p. 3), described as a new genus from the (Miocene?) fossil deposits of the Upper Amazon region of Ecuador, is not a subgenus of *Aylacostoma*. Reference of the group by later authors to *Aylacostoma* (=*Hemisinus*) is primarily due to the difficulty of complete separation of the genus *Doryssa* of the Pleuroceridae from *Aylacostoma* of the Thiaridae by shell characters alone. According to the shell characters of the original material, *Sheppardiconcha* is a synonym of *Doryssa*.

Family Pleuroceridae (in Asia)

Subfamily pleurocerinae

Genus *Oxytrema* Rafinesque, 1819

In the present state of our knowledge it is no longer possible to maintain the generic distinction of certain eastern Asiatic species from the genus *Oxytrema*, which has previously been considered

wholly North American. The generic name *Hua*, proposed by S. F. Chen (1943, p. 21) for the group of "*Melania*" *telonaria* Heude 1888, is a synonym of *Oxytrema* Rafinesque 1819. As is the case in both the Appalachian and Rocky Mountain regions of North America, the genus *Oxytrema* is represented in eastern Asia (Korea, China, and Thailand) by some species that are generally smooth (*Hua*) and some with strongly nodose or reticulate sculpture. Heude figured the female pleurocerine external anatomy of *Oxytrema* in 1890 in his excellent work on the Chinese fresh-water mollusks. Unfortunately, he misunderstood the structures of the females of such species as "*Melania*" *jacquetiana* Heude and called them male individuals. At present, Heude's mistake is easy to explain. The (female) egg-laying apparatus of these species (Heude 1890, pl. 43, fig. 5) is superficially identical in appearance to the (male) intromittent organ of certain operculate land snails of the subfamily Cyclophorinae (family Cyclophoridae) (see Heude 1890, pl. 42, fig. 12c), as a comparison of Heude's own figures will demonstrate. It is this extreme similarity in appearance that led Heude to an understandable misinterpretation and has effectively hidden the complete understanding of his critical discoveries for many years.

The present studies have corroborated those of Heude. The animals of *Oxytrema telonaria* (Heude) 1888 are dioecious; the sexes may be distinguished by the presence or absence of the female genital groove on the right side of the foot. There is a glandular, egg-laying pit at the terminal end of the groove a little above the right edge of the foot. The epithelium lining this groove is markedly different from that of the adjacent area and is easily distinguished in preserved material. The posterior edge of the groove is projected into the pit as a sort of papilla at its termination. The oviduct is not enlarged into a uterus; there are no embryos in the body behind the head. Animals of the following Asiatic species have been personally examined and found to exhibit the same pleurocerine reproductive anatomy with but little difference in minor details: *O. nodifila* (Martens) 1886, Han River, Korea (see pl. 11, fig. 3); *O. toucheana* (Heude) 1888, Min River, Fukien, China; *O. jacquetiana* (Heude) 1890, Shaohsing, Chekiang, China; *O. peregrinorum* (Heude) 1890, Fukien, China; *O. moutoniana* (Heude) 1890, Sa-Hsien, Fukien, China; *O. joretiana* (Heude) 1890, Chekiang, China; and *O. bailleti* (Bavay and Dautzenberg) 1910, Szechwan, China. How many of the other Asiatic species listed by S. F. Chen in these groups will prove to belong to *Oxytrema* can be determined only when their reproductive anatomy is examined. The presence of *Oxytrema* species in the recent fauna on both sides of the North Pacific Ocean demonstrates a geographic distribution similar to that of the genera *Viviparus* and *Anodonta*, sensu stricto. It is

evident also that the western American (Alaskan) region constituted the pathway of migration of these fresh-water mollusks between Asia and North America.

Genus *Paludomus* Swainson, 1840

With a short, ovate shell-shape corresponding to that of the American genus *Leptoxis*, the Asiatic genus *Paludomus* (Swainson, 1840, pp. 198, 340) also belongs to the subfamily Pleurocerinae. The anatomy of the animals of *Paludomus tanschaurica* (Gmelin) has been completely studied by Seshaiya (1934). The finding by Seshaiya of a tubular structure which he called a "penis" along the terminal portion of the primary gonoduct of the male must be discounted as a glandular discovery until it is proven to be an intromittent organ. As Seshaiya himself pointed out, it is not muscular as is the case of the similarly located and functional male organ of the Tiphobiinae. Seshaiya believed these animals oviparous, as he found no evidence of ovoviviparity in their anatomy. He did not, however, mention either the egg-laying groove or the pit. *Paludomus labiosus* (Benson) (?) from Thailand and *Paludomus maculatus* Lea from India (also members of the subgenus *Paludomus*, sensu stricto, with its concentric operculum) have been personally examined. The female animals are pleurocerine, with an egg-laying groove and pit in the side of the foot and without any brood pouch (see pl. 11, fig. 6). The true biological relations of the other subgenera such as *Hemimitra*, which differ markedly in shell and opercular characters, are still unknown or unrecorded.

Subfamily LAVIGERIINAE Thiele, 1929

Members of the subfamily Lavigeriinae Thiele (1929, p. 79) show the full dioecious mode of reproduction of the family. That is, there is a normal 1:1 sex ratio of males to females as in all other known members of the Pleuroceridae. The most important distinguishing character is the possession of a uterine brood pouch similar to that in the Viviparidae. As in the typical subfamily (Pleurocerinae), the males possess no intromittent structures whatsoever. Coincident to the development of ovoviviparity, the females have lost (at least do not possess) the egg-laying sinus and papilla characteristic of the Pleurocerinae. The name Semisulcospirinae Morrison (1952, p. 8) is a synonym of the earlier subfamily name Lavigeriinae.

Genus *Semisulcospira* Boettger, 1886

The genotype of *Semisulcospira* Boettger (1886, p. 4) is the well-known Japanese species *Semisulcospira libertina* (Gould) 1862. Examination of many specimens from the Hayakawa River, Honshu,

Japan, sent to the U. S. National Museum a few years ago by Captain Honess, U. S. Army Sanitary Corps, conclusively demonstrated that this species is ovoviviparous, as previously suspected. The head and snout of these snails are uncomplicated in either sex by external reproductive structures of any kind. Coitus is probably accomplished by apposition of the mantle edges, with perhaps some prolapsis of the genital duct openings. The lower part of the female reproductive duct (oviduct) is enlarged to form a functional uterus. It is thin-walled when fully distended with young and apparently is not glandular. The hundreds of embryonic young of uniformly small size developed at one time appear to be packed in axial rows, visible externally when the animal is removed from the shell and resembling the conglutinates of glochidia of the North American fresh-water mussel genus *Strophitus*. In some cases the young nearest the oviduct are not fully developed, showing that development of the ova is at least partly progressive as the young approach the uterine mouth. On the other hand, the great uniformity of size of all the fully developed young, with shells of about 2 whorls, would indicate a definite seasonal, mass release of the young. At any rate, there is no indication of any continued growth to large size of a few embryos at a time or continued parturition over a long season or throughout the year as in certain genera of the family Thiaridae.

Recently, Corp. W. E. Old of the U. S. Army Signal Corps sent four species of "*Melania*" from Korea to the U. S. National Museum. Examination of the animals by both R. T. Abbott and the author has proven that "*Melania*" *nodifila* Martens is an *Oxytrema* as noted above, while the species *gottschei* Martens, *nodiperda* Martens, and *graniperda* Martens (1905) are members of the genus *Semisulcospira*. The geographic range of *Semisulcospira* across continental Asia is imperfectly known and in need of continued research.

Family Pleuroceridae (in Africa)

Subfamily Pleurocerinae

Genus *Potadoma* Swainson, 1840

The genotype of *Potadoma* Swainson (1840, pp. 200, 341), *P. freethii* (Gray), must be examined to completely clear up the position of this genus. Pilsbry and Bequaert (1927) have reported that these snails are apparently oviparous, with the edge of the mantle smooth and even. They compare these species to some species of the American genus *Pachychilus*. If *Potadoma* is oviparous as reported, with the egg-laying groove, it belongs in the subfamily Pleurocerinae, and the subfamilies

Potadominae Pilsbry and Bequaert and the Paludominae are included synonyms. In addition to the species called *Potadoma* by Pilsbry and Bequaert, some of the species they called "*Melanoides*" also belong to *Potadoma* of Swainson. "*Melanoides*" species such as *ignobilis* (Thiele) (Pilsbry and Bequaert, 1927, p. 278, pl. 26, figs. 1, 2) are smooth; others such as *medjeorum* Pilsbry and Bequaert (1927, p. 283, fig. 47) and *tornata* (Martens) (Pilsbry and Bequaert, 1927, p. 283, fig. 48) possess strong spiral sculpture. Still others, such as *wagenia* Pilsbry and Bequaert (1927, p. 262, pl. 22, figs. 14–16), *crawshayi* (E. A. Smith) and *mweruensis* (E. A. Smith) (Pilsbry and Bequaert, 1927, pp. 264–265, pl. 22, figs. 19–22) show strong plicate to cancellate shell sculpture. The total picture of sculpture in this genus seems exactly parallel to that seen in Appalachia, western America, and eastern Asia in the genus *Oxytrema*.

Genus *Limnotrochus* E. A. Smith, 1880

1880. *Limnotrochus* E. A. Smith, 1880b, p. 425. (Genotype, *Limnotrochus thomsoni*, E. A. Smith, 1880.)

Genus *Paramelania* E. A. Smith, 1881

1881. *Paramelania* E. A. Smith, 1881b, p. 559. (Genotype, *Paramelania damoni* E. A. Smith, 1881, by subsequent designation by Pilsbry and Bequaert, 1927, p. 320.)

Genus *Spekia* Bourguignat, 1879

1879. *Spekia* Bourguignat, 1879, p. 27. (Genotype, *Spekia zonatus* (Woodward), 1859, by monotypy.)

Pilsbry and Bequaert have said that, as far as known, the three above-named genera are oviparous. If complete study of the animals confirms this and reveals the characteristic egg-laying pit in the side of the foot, these Lake Tanganyika forms are also Pleurocerinae. Moore (1899a, p. 171) found neither an external groove nor a brood pouch of any type in the females of *Spekia zonata* (Woodward) examined by him. This condition seems identical in appearance to that of those North American members of the pleurocerine genus *Oxytrema*, in which the female egg-laying groove is not demarcated structurally and can only be seen functionally as a linear depression in the skin during the breeding season.

Subfamily LAVIGERIINAE Thiele, 1929

The statement of Pilsbry and Bequaert (1927, p. 300) in regard to the ovoviviparity of the mixture of species they called "*Melanoides*" is in need of clarification. They left the problem unsolved when they said: "*Typhobia*, *Bathanalia*, and *Lavigeria* are viviparous, having the

last part of the oviduct enlarged to form a brood pouch in the mantle, as in *Melanoides* and *Viviparus*." The fact is that *Melanoides* does not have a uterine brood pouch as in the family Viviparidae. True *Melanoides* species have the subhaemocoelic brood pouch in the back of the neck, with the brood pouch pore on the right, as in all other members of the Thiaridae.

If Pilsbry and Bequaert actually saw uterine brood pouches in the animals of any African species of "*Melanoides*," they probably were dealing with members of the subfamily Lavigeriinae, of an unnamed genus. In this connection, the possibility should be stated frankly that the subfamilies Lavigeriinae and Tiphobiinae may in the future prove to be biologically confluent. Much more study of the animals of African fresh-water species both in and out of Lake Tanganyika is needed to prove or disprove this possibility. As defined above, the subfamily Lavigeriinae includes those genera of pleurocerid snails in which the males have no intromittent organ and the females possess uterine brood pouches.

Genus *Lavigeria* Bourguignat, 1888

The genus *Lavigeria* Bourguignat (1888, p. 33) is another of the peculiar pleurocerid forms found in Lake Tanganyika. In addition to the shell characters, this genus differs from others by its operculum, which is modified by partial uncoiling to a subspiral form. Moore 1899b, p. 192, pl. 20, fig. 6) has furnished anatomical studies of the species *Lavigeria coronata* Bourguignat. He called the animal "*Nassopsis nassa* Woodward," while Pilsbry and Bequaert have referred this anatomical study to the genotype which they designated, namely: *Lavigeria grandis* (E. A. Smith) 1881. Moore's figure of the shell proves he studied the species *coronata*. He found that this genus possesses a uterine brood pouch similar to that of *Viviparus* and of the Tiphobiinae. According to him, the males do not possess any secondarily developed intromittent organ such as is found in the mantle edge of the males of *Tiphobia*.

Genus *Bourguignatia* Giraud, 1885

1885. *Bourguignatia* Giraud, 1885, p. 193, pl. 7, figs. 5–7. (Genotype, *Bourguignatia imperialis* Giraud, 1885, by monotypy.)

Genus *Edgaria* Bourguignat, 1888

1888. *Edgaria* Bourguignat, 1888, p. 33. (Genotype, *Edgaria paucicostata* (E. A. Smith), 1881, by subsequent designation by Pilsbry and Bequaert, 1927, p. 328.)

The shells of the *Bourguignatia*, *Lavigeria*, *Edgaria*, and *Paramelania* complex of Lake Tanganyika are almost identical in general characters; however, there are two distinct types of opercula known in the group.

Our present lack of anatomical knowledge of all but *Lavigeria* makes it impossible to say whether two or more subfamilies are represented in this complex of shells inhabiting the rocky shorelines of Lake Tanganyika.

Genus *Bythoceras* Moore, 1898

1898. *Bythoceras* Moore, 1898c, p. 452. (Genotype, *Bythoceras iridescens* Moore, 1898, by monotypy.)

These shells from deeper waters of Lake Tanganyika are also very similar to those of the *Lavigeria* complex; their opercula differ from those of *Lavigeria* in being secondarily concentric around a paucispiral nucleus. The general statement by Moore (1898d) that *Bythoceras* is much more like *Tanganyicia* in anatomy than ("*Nassopsis*"=) *Lavigeria* is in need of corroboration or clarification. Neither is it clear from Moore's subsequent statements and figures (1899b) whether *Bythoceras* is ovoviviparous or not.

The final allocation of these names and also of *Paramelania* and the subfamily name Paramelaniinae must await the complete recording of shell, opercular, and reproductive characters of all members of the *Lavigeria* complex of Lake Tanganyika. If the reproductive anatomy proves identical, Paramelaniinae (Moore, 1898b, p. 315) will supersede the name Lavigeriinae (Thiele, 1929, pp. 79, 83) used at this time.

Subfamily TIPHOBIINAE Moore, 1898

These are pleurocerid snails modified in the males by the development of a secondary, eversible "penis" or vergic structure in the mantle edge near the end of the vas deferens. As far as known, these are the only "Melanian" snails of any kind that possess any intromittent structures whatsoever. The females are ovoviviparous, with the terminal portion of the oviduct modified into a uterine brood pouch for the young. At present, our knowledge—or lack of knowledge—indicates that the Tiphobiinae are solely African in geographic distribution, parallel to but not identical with the Asiatic and African subfamily Lavigeriinae.

Genus *Tiphobia* E. A. Smith, 1880

The genotype of *Tiphobia* E. A. Smith (1880a, p. 348, pl. 31, fig. 6), *T. horei* E. A. Smith, 1880, possesses the reproductive characters of the subfamily, as defined above, according to the studies of Moore (1898a). The statement of Pilsbry and Bequaert that the characters of the Tiphobiidae do not distinguish them from the Melaniidae is based on their misunderstanding of the true nature of the brood pouch of the Thiaridae ("Melaniidae"). *Tiphobia* is one of the endemic genera of Lake Tanganyika, with a spinose shell and a

secondarily concentric operculum. Its complete biological relationship with the other Tanganyika genera and with extra-Tanganyika forms must be clarified by future studies.

Genus *Bathanalia* Moore, 1898

The genotype, *Bathanalia howesi* Moore, 1898, is stated by Moore (1898a) to be "almost identical anatomically with *Tiphobia horei*." This genus differs from *Tiphobia* by shell characters such as height of spire and the perforate columella. In addition, *Bathanalia* possesses an unmodified (paucispiral) operculum.

Family Thiaridae

The pattern of reproduction is the same for all known members of the family Thiaridae. A high degree of specialization in this one character is indicated by this observed pattern of ovoviviparous parthenogenicity. In other words, there is no male individual known in this entire family of snails. To my knowledge, the parthenogenesis of the Thiaridae has not been examined cytologically to determine whether it is haploid or diploid.

There is required only one individual (any individual) to start a new population or colony if it reaches a new fresh-water locality by stream capture or by adventitious transportation. The resultant ability of these snails theoretically to spread more rapidly may partly explain their wider distribution in suitable habitats on islands in both the Pacific and the West Indies and their wider expansion southward across South America than that exhibited at present by the family Pleuroceridae. Certain corollaries are assumed in this theoretical explanation of the differences and peculiarities of distribution of the two fresh-water families of Pleuroceridae and Thiaridae. Structurally, the animals of these families are relatively primitive, exceedingly so as regards their fundamental reproductive characters. Without any proof to the contrary, we may assume them to be of approximately equal antiquity, geologically speaking. Reasoning from the specialized pattern of reproduction of the Thiaridae, we may logically argue that they are the younger group evolved from the older ancestral type represented now in fresh water by the Pleuroceridae. If this be true, the younger has outstripped the more primitive older type in geographic expansion over geologic time from the era of their differentiation up to the present. If the Thiaridae were ever in North America we must assume that they are no longer represented there because the conditions of existence are not now or were not, during some previous geologic era, favorable to their continued existence in those northern areas. Their expansion across the North American continent may be

unrepresented in any fossil record, known or yet undiscovered, because successfully living fresh-water mollusk species seldom undergo fossilization. They usually enter the fossil record only when a habitat change brings about the extinction of populations or species. On the other hand, the present geographic distribution of the Thiaridae argues for their greater ability to spread across oceanic areas on island stepping stones without the necessity for any continuous "land bridges."

There is one important taxonomic problem present in the Thiaridae that has not often been acknowledged in the study of these or any other parthenogenetic animal species. We know by observation the great variability of individuals within the species of the dioecious type such as the Pleuroceridae. This variability is the greatest single factor contributing to confusion in past and present studies of these fresh-water shells. The variability of individuals of the related Thiaridae may be either increased or decreased because of their reduction to unilateral ancestry. What we actually have in the entire family of the Thiaridae is the possibility of clone formation in every existing population of these animals. These is no biparental or cross-inheritance control or check on individual variation in their present parthenogenetic state. Wise indeed is the scientist who can tell whether a clone is a species or not, and be right every time, in the case of the Thiaridae.

Family Thiaridae (in the Americas)

The earliest generic name for any of the indigenous American species of this family is *Aylacostoma* Spix (1827, p. 15, pl. 8). This manuscript name of Spix was first published in the synonymy of both *Melania tuberculata* Wagner (= *Aylacostoma tuberculatum* Spix) and *Melania scalaris* Wagner (= *Aylacostoma glabrum* Spix) in connection with the species description, and also on plate 8 (Spix, 1827) without the indication of synonymy. This is in the first edition (Munich) of plates, not the second edition (Leipsic). As a manuscript name of Spix, published in direct connection with two validly described and figured species, *Aylacostoma* is valid and available. The genotype, by subsequent designation by Morrison (1952, p. 8), is *Melania scalaris* Wagner (= *Aylacostoma glabrum* Spix). This species, as comparison of the figures will demonstrate, is that form called *behnii* by Reeve (1859–1861, pl. 2, fig. 8) in his 1860 monograph on *Hemisinus*.

Swainson (1840, pp. 200, 341) was next to furnish a name for American Thiaridae. *Hemisinus* is his generic name given to the species *lineolata* Gray from Jamaica. The later emendations, *Aulacostoma* Agassiz 1846 and *Semisinus* Crosse and Fischer 1885, are both

unnecessary and invalid under present international rules of nomenclature. *Basistoma* Lea (1852, p. 295) is exactly equivalent biologically to *Aylacostoma*, being based on the same type of shell from South America. *Verena* H. and A. Adams (1854, p. 308) differs from the typical *Aylacostoma* group in shorter shell outline and in sculpture.

Genus *Cubaedomus* Thiele, 1928

This genus (Thiele, 1928, p. 401), based on the species *brevis* Orbigny from Cuba, is the only American group clearly and generically distinct from *Aylacostoma* on shell characters. The shell is ovate-conic, with a trace of nodulous coronate sculpture on the upper slope or shoulder of the body whorl. There is no columellar notch or sinus in the aperture, which is evenly rounded below (anteriorly). The operculum is paucispiral. Animals of this species, dried in the shells, were recently boiled up in water (softened) and personally examined. These specimens (USNM 407991) were collected by Jaume from Río "Los Cayos", Bahia Hondo, Pinar del Río, Cuba. The mantle is fringed. The embryonic young are relatively large, and there were only two in the subhaemocoelic brood pouch in the neck region at one time in the material examined (pl. 11, fig. 19). Proof that this genus belongs to the family Thiaridae gives us another excellent example of concurrent and convergent evolution. Both Pilsbry (1893) and Aguayo (1944, p. 69) have previously considered the species *brevis* Orbigny of Cuba congeneric with ("*Potamanax*"=) *Pachychilus* (*Oxymelania*) *pilsbryi* (Martens) of the Guatemala region, a member of the Pleuroceridae, because of the almost identical shell characteristics of the two species.

Genus *Aylacostoma* Spix, 1827

Subgenus *Hemisinus* Swainson, 1840

Genotype: (*Melania lineolata* Gray =) *Aylacostoma* (*Hemisinus*) *lineolatum* (Gray) 1828.

This group of elongate-ovate or ovate-conic shells, almost completely lacking macroscopic spiral sculpture, includes one or two species from Cuba, the genotype from Jamaica, and a few other species of Central and South America from Panamá to Ecuador and Perú.

Subgenus *Aylacostoma* Spix, 1827, sensu stricto

Genotype: (*Aylacostoma glabrum Spix*=) *Aylacostoma* (*Aylacostoma*) *scalare* (Wagner) 1827.

This typical group includes one species from the Atlantic side of Central America, one species from the Pacific drainage in the Darién region of Panamá, and numerous species from the Magdalena, Orinoco, Amazon, and southern Brazil regions of South America.

These shells have spiral sculpture more or less prominent on most of of the whorls, and in some of the species there is a peculiar swelling or expansion of the body whorl of adults. The female reproductive anatomy and embryos (from the brood pouch) of the Central American species *Aylacostoma ruginosum* (Morelet) were figured by Crosse and Fischer (1892, pl. 49, fig. 10). In these figures the brood pouch relation is not clearly indicated; it was not fully understood to be a separate adjunct to the primary female reproductive system. Hinkley (1920, p. 47) also has recorded the reproduction and ecology of this species. He says:

> Their trail was made by burrowing instead of crawling on the surface as with other forms. They burrowed somewhat like a mole, and often the little mole-like ridge could be followed quite a distance, and the mollusk found working under cover.
>
> It is a viviparous genus. When cleaning these shells the embryos run from one to three to the individual. None were noticed with more than three.

Hinkley's observations on the embryos are corroborated by dried animals, received with the shells (USNM 218018) from Hinkley, which show two large young in situ in the brood pouch. These specimens are from Lake Ysabal, Jocolo, Guatemala.

Subgenus *Longiverena* Pilsbry and Olsson, 1935

Genotype: (*Aylacostoma tuberculatum* Spix, 1827=*Melania tuberculata* Wagner, 1827, not *Melania tuberculata* (Müller) 1776=) *Aylacostoma* (*Longiverena*) *tuberculatum* Spix, 1827, by subsequent designation by Morrison, 1952.

This subgeneric group of *Aylacostoma* species possesses prominent longitudinal sculpture in addition to the spiral lirae present on the shells of *Aylocostoma*, sensu stricto. In this way, the upper spire whorls may greatly resemble the corresponding portion of the shell of some species of *Doryssa* described from the same general region. More study is required for proof, but this general resemblance of *Doryssa* and *Longiverena* shells may be another outstanding example of concurrent and convergent evolution of the families Pleuroceridae and Thiaridae.

Pilsbry and Olsson (1935, p. 11) did not formally designate any of the originally included species, recent or fossil, as genotype, so we designated the living species *tuberculatum* in order that the animal characters of the group may be used to correctly place this unit in the total biological picture.

Subgenus *Verena* H. and A. Adams, 1854

Genotype: (*Melania crenocarina* Moricand=) *Aylacostoma* (*Verena*) *crenocarina* (Moricand).

This fourth South American group, *Verena*, has been considered distinct by most authors. Its principal known distinguishing character is the possession of strong, undulate or scalloped spiral ridges on the post-nuclear whorls. Dr. Olsson of the Academy of Natural Sciences of Philadelphia has recently found species in the fossil record from the upper Amazon region that prove the existence of *Verena* in that area for considerable time. These fossil species possess shells with sculpture identical in type to that of *crenocarina* (Moricand), but, unlike that living species, show shell outlines more or less completely transitional to the high-spired outline of *Aylacostoma*, sensu stricto.

Genus *Tarebia* H. and A. Adams, 1854

One Asiatic species, probably *Tarebia lateritia* (Lea) from the Hawaiian Islands, has recently been introduced to American waters with aquarium plants. This species was first discovered living feral in Lithia Sulphur Springs, near Tampa, Fla., in December 1947 by C. W. Cooke of the U. S. Geological Survey. It was not there in March 1940 on the occasion of an earlier complete collection of mollusk species by Dr. Cooke from that spring. This kind of introduction is highly dangerous to public health because this Asiatic type of snail is one of the primary intermediate host species of the human lung fluke (Paragonimiasis).

Family Thiaridae (in Asia)

Genus *Thiara* Röding, 1798

This genus (Röding, 1798, p. 109) was not originally monotypic. It included two valid specific names, *amarula* (Linnaeus) 1758 (Chemnitz, 1786, pl. 134, figs. 1218, 1219) and *cancellata* Röding 1798 (Chemnitz, 1786, pl. 134, figs. 1220, 1221), as well as three nomina nuda. Hermannsen (1849, p. 576) did not explicitly state that *amarula* Linnaeus was the type. In Latin, he said it was a genus "of the type of." However, Brot (1874, p. 7) formally designated *amarula* the genotype. In the same monographic work he named two other groups which are synonyms of *Thiara*. *Tiaropsis* Brot (1874, p. 7), based on the genotype species *winteri* von dem Busch (1842, p. 1, pl. 1, figs. 1, 2), and *Plotiopsis* Brot (1874, p. 7), based on the genotype species *balonnensis* Conrad (1850, p. 11), both possess the same shell characters as *Thiara*, differing principally in height of spire and size of shell. At present these differences are only considered of specific value. Another recently created synonym is *Pseudoplotia* Forcart 1950, with the species *scabra* Müller 1776 as originally designated genotype.

Subgenus *Thiara* Röding, 1798, sensu stricto

Genotype: Thiara (*Thiara*) *amarula* (Linnaeus), 1758.

The animals of *Thiara* spp. from Szechwan, China, Mindanao, Philippine Islands, and Okinawa, Ryukyu Islands, have been examined by me and found to possess the reproductive structures described above as distinguishing characteristics of the family (pl. 11, figs. 9, 11).

Subgenus *Setaeara* Morrison, 1952

Genotype: (*Thiara cancellata* Röding 1798=) *Thiara* (*Setaeara*) *cancellata* Röding 1798.

The genotype has been known for many years under the name of *setosa* Swainson because the far earlier name of Röding has not hitherto been critically examined. These shells possess stronger spiral sculpture than those of *Thiara*, sensu stricto, and the "crown" of spines on the shoulder of the whorls is continued upward as a set of cuticular setae, easily broken off, and almost always missing from imperfect shells. This group of only a few species was proposed as a subgenus (Morrison, 1952, p. 8) until animal characters are found that confirm its separation from *Thiara*, sensu stricto, by means of the shell.

Genus *Tarebia* H. and A. Adams, 1854

Genotype: (*Melania semigranosa* von dem Busch =) *Tarebia semigranosa* (von dem Busch) 1842, by subsequent designation by Morrison, 1952.

Reexamination of the type designation of this genus by Brot (1874, p. 7) shows it to be completely inoperative. His statement that "*granifera*" is the type refers to *Melania granifera* von dem Busch, the only such specific name originally included by H. and A. Adams. To the best of my knowledge, *T. granifera* H. and A. Adams is still a nomen nudum. This nomen nudum is proven not to be the same as *Melania granifera* of Lamarck by H. and A. Adams, who listed Lamarck's specific name separately and distinctly as a member of the genus *Plotia*. One of the valid, originally included species was designated as genotype (Morrison, 1952, p. 8) in order to correctly and legally fix *Tarebia* upon the group of thiarid snails to which it has been restricted and applied since the time of Brot (1874).

The animals of *T. lateritia* (Lea) from China, of *T. granifera* (Lamarck) from the Philippines, and, more recently, of the *Tarebia* colony accidentally introduced to Lithia Sulphur Springs, near Tampa, Fla., have been examined for the reproductive characters and proven thiarid.

Genus *Sermyla* H. and A. Adams, 1854

Genotype: (*Melania mitra* Dunker =) *Sermyla tornatella* (Lea) 1850.

Recent examination of the animals of *S. kowloonensis* S. F. Chen 1943 and of *S. mauiensis* (Lea), from China and the Hawaiian Islands respectively, proves this genus typically thiarid, as most authors have considered it. These shells possess arcuate, longitudinal sculpture on the upper (posterior) portion of the whorls, strongly contrasting with the spiral lirae below (anterior). They are relatively short-spired.

Genus *Stenomelania* Fischer, 1885

Genotype: (*Melania aspirans* Hinds=) *Stenomelania aspirans* (Hinds).

Stenomelania Fischer (1885, p. 701) is a thiarid genus of elongate shells with the spire sometimes exceedingly attenuate and sharp-pointed, when not eroded away. Members of this genus possess the brood pouch typical of the family, that holds the eggs until they develop into veligers. Seshaiya (1940, p. 331) has shown that these snails, living in estuarine habitats, release the embryonic young into the water in the veliger stage. There is thus a free-swimming larval stage in the life history. These observations recently have been corroborated in the case of certain Philippine species of the genus by R. T. Abbott. The species *M. aspirans* is the genotype by monotypy. Another species, *M. hastula* (Lea), is the genotype by original designation of the synonymous generic name *Radina* of Preston (1915, p. 10).

Genus *Melanoides* Olivier, 1804

Genotype: (*Melanoides fasciolata* Olivier=) *Melanoides tuberculata* (Müller) 1776.

The shells of *Melanoides* are elongate-conic, of a number of regularly increasing whorls. The spire is usually twice the length of the aperture, or more. The sculpture is smooth to finely or coarsely tuberculate, in different species, without any material difference between the younger and older portions of the shell. The operculum is clearly paucispiral, with the nucleus so near the base that in some cases it may approach the subspiral condition.

A personal check on available material in the U. S. National Museum collections has shown that the following species belong to *Melanoides*, agreeing exactly in the thiarid type of ovoviviparous, parthenogenetic reproduction: *M. chinensis* (Nevill), China; *M. suifuensis* S. F. Chen, Szechwan, China; *M. turriculus* (Lea), Leyte, Philippine Islands; *Melanoides* sp., Rota, Marianas Islands; *M. vainafa* (Gould), Ofu, Samoa; and *M. indefinata* (Lea), Oahu, Hawaiian Islands.

Genus *Sulcospira* Troschel, 1857

Genotype: (*Melania sulcospira* Mousson=) *Sulcospira sulcospira* (Mousson).

Recorded as "also viviparous," this group must be studied further before its true relationships to the other genera from the Malayan region can be proved. Troschel (1857, p. 114) has recorded the radular characters; the shell appears similar to certain species of *Brotia*, to *Tylomelania*, or to immature individuals of *Balanocochlis*. Until the animal characters are reexamined, *Sulcospira* may be left tentatively in the "*Melanoides* complex."

Genus *Balanocochlis* Fischer, 1885

Genotype: (*Melania glans* von dem Busch=) *Balanocochlis glans* (von dem Busch) 1842.

Philippine animals of this species, collected by R. T. Abbott at San Ramon, Mindanao (USNM 543951), have recently been examined. These animals prove the genus to be thiarid. There is a minute brood-pouch pore bordered with "flaps," similar to that figured for *Melanoides turriculus* (pl. 11, fig. 14), low on the right side and close to the fringed mantle edge. Apparently there are many hundreds of minute eggs in the brood pouch. Either they develop as numerous, small, equal-sized young shells as in certain *Melanoides* species, or they may be released in the veliger stage for a free-swimming larval period, as is known for the genus *Stenomelania*. The material examined, which contained only the eggs, is not conclusive on this point. In any case, the shell and opercular characters are distinct enough from any other thiarids known to maintain the full generic separation of *Balanocochlis*. The earlier name *Melania inermis* Lesson 1830 was preoccupied by Gray in 1825; the later name *M. siccata* von dem Busch 1843 probably represents young of the species *Balanocochlis glans*.

Genus *Tylomelania* P. and F. Sarasin, 1898

Genotype: Tylomelania neritiformis P. and F. Sarasin.

This subpaludomiform group of shells only appears as a separate development of shell outline and proportions; they have the same type of "paleomelanian" operculum and the same general radular characters as do *Antimelania* and *Brotia*. The animals of all the groups must be completely and carefully reexamined before the genera (and the distinctions of the genera) of the "Melanoides complex" of the Thiaridae can be properly organized or understood. Shell, radular, and opercular characters of this group were carefully recorded by the Sarasins (1898, p. 52, pl. 4, figs. 56, 57; pl. 8, figs. 110, 111; pl. 9, fig. 115), but they did not examine the details of the reproduction of *Tylomelania*.

Genus *Antimelania* Crosse and Fischer, 1892

Genotype: (*Melania variabilis* Benson 1836 (not *Melania variabilis* Defrance 1823)=) *Antimelania costula* (Rafinesque) 1833.

As the well-known but preoccupied and preceded name for the genotype implies, the shell sculpture of members of this genus is variable. These shells are similar to *Melanoides* but usually larger in size, with the sculpture bolder when present. The operculum is paleomelanian, often with about 6 turns in contrast to that of *Melanoides* with about 2 turns. The apex or nuclear whorl of these shells is perfectly symmetrical in uneroded individuals. The aperture is more-or-less regularly rounded at the base, without a forward projecting rounded angle as in *Brotia*.

Specimens of *Antimelania soriniana* (Heude) collected in 1940 by Dr. H. T. Chen at Tai-Mo-Shan, Kwangtung, China, possess a paleomelanian operculum (with large nucleus) as in Heude's figures (1890, pl. 41, figs. 6, 6a). They were all ovoviviparous, parthenogenetic females containing hundreds of minute young in the brood pouch, which is enormously expanded into the body cavity behind the head. They possessed a narrow genital groove terminating abruptly on the right side of the foot, without any trace of the pleurocerine type of egg-laying sinus.

Apparently Pilsbry and Bequaert (1927, p. 300) did not know that the specific name *variabilis* was preoccupied when they designated it the genotype of *Antimelania* (Crosse and Fischer, 1892, p. 313). A search for the correct name to use in replacement led to the discovery that *costula* Rafinesque (1833, p. 166) is clearly recognizable as identical to Benson's *variabilis*.

Moore (1899a, p. 161) has recorded the brood-pouch ovoviviparity of "*Melania*" *episcopalis* (Lea). His figure (pl. 14, fig. 13) of the female *Antimelania episcopalis* (Lea) agrees with our observations on the genus *Antimelania*. The figure given by him of a "male" animal of this same species is either a nongravid or nonbreeding female of the same species, or a female of the pleurocerine genus *Oxytrema* with only the genital groove and egg-laying pit in the side of the foot. Moore (1899a, p. 163) mentions the presence of males in *Tanganyicia* and "*Melania*," but nowhere proves it. The presence of any males in this family is still not proved.

Genus *Brotia* H. Adams, 1866

Genotype: (*Melania pagodula* Gould 1847 (not *Melania pagodulus* Reeve 1860)=) *Brotia pagodula* (Gould) 1847.

Shells of this genus are elongate-conic, of variable sculpture, and with the columellar angle of the basal lip of the aperture produced

slightly forward. The operculum is of the paleomelanian type, of many (6 or 8) turns, and, in the species seen, is considerably smaller than the aperture. The perfect apex of the shell (nuclear whorl) is asymmetrical. Specimens of the animals of *Brotia baccata* (Gould) and the adult and embryonic shells of three other species of *Brotia* from the Salween River of Thailand and Burma have been personally examined. In the species *baccata* there is a well-developed, deep genital groove down the right side of the foot that abruptly turns inward to become the entrance (or "birth pore") of the brood pouch. This brood pouch is very large, crowded with a great many relatively small young of uniform size. The single character of the embryonic shell, or the apex (when perfect) of the adult shell, that characterizes *Brotia* is the asymmetry. It appears as if each shell in its development is interfered with by a yolk sac (?) in the position of the apex to keep that apex soft, while the rest of the embryonic whorls develop normally and symmetrically, and then the apex collapses to a line below the curve of spiral symmetry. This may very well be connected with a secondary development in the brood pouch to insure a "nurse" type of nutrition of the young.

Synonyms of *Brotia* include *Acrostoma* Brot 1874, *Brotella* Rovereto 1899, *Paracrostoma* Cossman 1900, with the genotype *hugeli* Philippi, and *Wanga* S. F. Chen (1943, p. 21), based on the species *Melania henriettae* Gray (1834, pl. 13, fig. 2). In this connection it should be mentioned that the original figure of *henriettae* is poorly drawn and does not show the generic character of the slightly produced columellar angle of the aperture. This fault is corrected in the figure of the holotype published by Yen (1942, p. 204, pl. 15, fig. 66). In fact it is possible that the originally published locality of *henriettae* ("China") is at fault, and this may be the same species as *baccata* (Gould) of the Salween River and some of its tributaries.

Genus *Fijidoma* Morrison, 1952

Genotype: (*Fijidoma laddi* Morrison 1952)=*Fijidoma maculata* (Mousson) 1865, by original designation.

Fijidoma Morrison (January 1952) antedates by only a few months the synonymous generic name *Veloplacenta* Hubendick (August 1952), which was based on the same species of thiarid snail. These freshwater snails from Viti Levu in the Fiji Islands, superficially very similar in shell outline to those of the southeast Asiatic genus *Paludomus*, were named in allusion to that similarity. They have rather smooth, subglobose, neritiform shells with a few rather rapidly increasing, well-rounded whorls separated by a deep suture. The shell has fine spiral sculpture and regular flammules or rows of squarish dots (interrupted flammules) of red in the ground color. The aper-

Explanation of Plate 11

1, *Melanopsis dufourii* (Ferussac), female, from the right side showing egg-laying groove and the "ovipositor" in pit on right side of foot, from Elche, Alicante Province, Spain (USNM 515845).

2, *Oxytrema canaliculatum undulatum* (Say), female, showing egg-laying groove and pit in right side of foot, from Kentucky River, Clifton, Ky. (USNM 597434).

3, *Oxytrema nodifila* (Martens), female, as in fig. 2, from Han River, Kwang-jang-in, Korea (USNM 597451).

4, *Pleurocera zonalis* (Rafinesque) (=*Melania obovata* Say), female, as in fig. 2, from Kentucky River, Clifton, Ky. (USNM 595969).

5, *Oxytrema bulbosa* (Gould), female, as in fig. 2, from tributary of John Day River, 10 miles east of Austin, Grant County, Oreg. (USNM 473801).

6, *Paludomus labiosus* (Benson) (?), female, as in fig. 2, from roadside run north of Lampang, Thailand (USNM 361267).

7, *Oxytrema deshayesiana* (Lea), female, as in fig. 2, from Tennessee River, near Florence, Ala. (USNM 601564).

8, *Planaxis sulcatus* (Born), ovoviviparous and parthenogenetic female showing egg-transfer groove and brood-pouch pore ("birth pore") on side of neck, and subhaemocoelic brood pouch in back of head and neck, from Romurrikku Island, Bikini Atoll, Marshall Islands (USNM 585106).

9, *Thiara* sp., female, showing brood-pouch pore and numerous young in the subhaemocoelic brood pouch, from Mindanao, Philippines (USNM 434144).

10, *Brotia baccata* (Gould), female, showing deep egg-transfer groove on right side and subhaemocoelic brood pouch with hundreds of relatively small young, from Salween River, Ban Mae Hick, Burma (USNM 420467).

11, *Thiara* sp., female, as in fig. 9, showing the anus, oviduct opening, and brood-pouch pore relations, from Naga, Okinawa, Ryukyu Islands (USNM 601311).

12, *Melanoides* sp., female, as in fig. 9, with unpigmented shallow "groove," and numerous, equal-sized, small young, from Palo, Leyte, Philippines (USNM 573572).

13, *Tarebia lateritia* (Lea), female, as in fig. 9, with numerous small young, from Caminiwit Point, Mindoro, Philippines (USNM 487583).

14, *Melanoides turriculus* (Lea), female, as in fig. 9, with numerous very small young in pouch, from Caminiwit Point, Mindoro, Philippines (USNM 487582).

15, *Melanoides* sp., female, as in fig. 9, with a very few proportionately enormous young developed in the subhaemocoelic brood pouch, from Manganyama, Rota, Marianas Islands (USNM 593472).

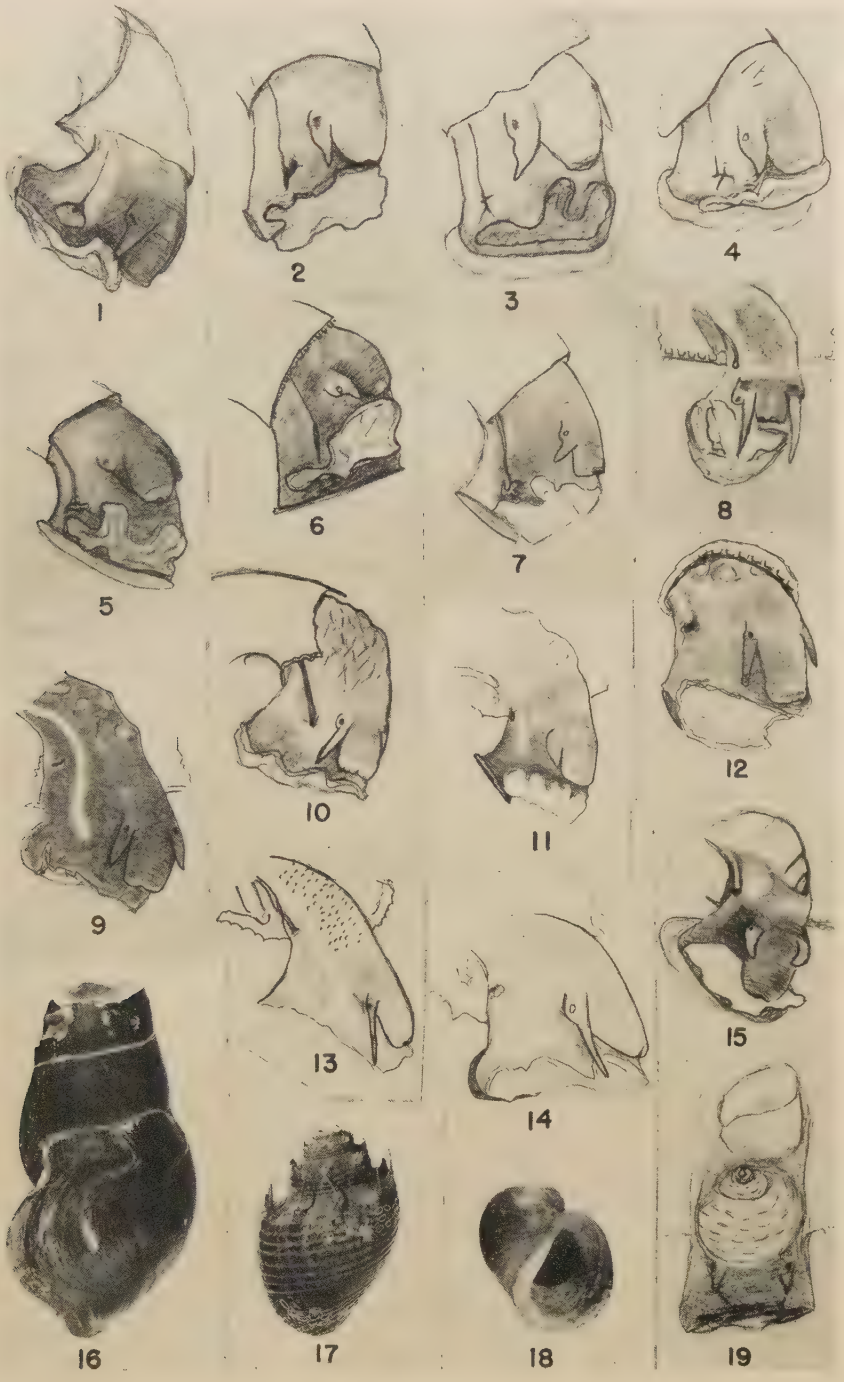
16, *Pachychilus* (*Pilsbrychilus*) *dalli* Pilsbry, old individual showing 3 consecutive peristomes to prove continuity of sinuous lip character of adults, from Tehuantepec, México (USNM 133197).

17, *Thiara* (*Setaeara*) *cancellata* Röding, fresh shell showing epidermal spines, from Siaton, Negros Oriental, Philippines (USNM 597436).

18, *Fijidoma maculata* (Mousson) (=holotype of *laddi* Morrison) from Viti Levu, Fiji Islands (USNM 597433).

19, *Cubaedomus brevis* (Orbigny), ovoviviparous and parthenogenetic female (sketched from dried material), showing only 2 embryonic young of relatively enormous size in subhaemocoelic brood pouch, from Río los Cayos, Bahia Honda, Pinar del Río, Cuba (USNM 407991).

(Animal sketches not drawn to scale; figs. 16, 17 slightly reduced; fig. 18 enlarged approximately 2 times.)



(For explanation see opposite page)

ture is nearly semicircular with a broad, flattened, white columella. The operculum is similar to that of *Melanoides;* thin, corneous, and paucispiral, of less than two turns. A few small-to-medium, but not uniform-sized, young shells found dried inside some adult specimens indicated that this genus belongs to the Thiaridae, although the animals were not available for study.

***Fijidoma maculata* (Mousson) 1865.**

Publication of the independent investigation by Hubendick of shells and animals in the collections of the Bernice P. Bishop Museum has brought to my attention the following synonymy:

Ampullacera maculata Mousson (1865, p. 203).
Ampullacera maculata Crosse (1865, p. 432, pl. 14, fig. 10).
Ampullarina maculata Nevill (1878, p. 249).
Salinator maculata Hubendick (1945, p. 108).
Fijidoma laddi Morrison (Jan. 1952, p. 8).
Veloplacenta maculata Hubendick (Aug. 1952, pp. 179–184, pl. 1).

In this species the body whorl is enormous, so that the height of the spire is less than one-fourth the height of the aperture. The aperture is roughly semicircular, with both upper and lower (anterior and posterior) angles well rounded. Nuclear whorls smooth; early postnuclear whorls sculptured by incised spiral lines between broad, flat rib-areas, crossed by microscopically fine (cuticular) growth lines. The spiral sculpture becomes obsolete or absent on the body whorl, persisting longest just below the suture and in the columellar region. The columella is rather straight, broad, heavily callused, and flattened or a little excavated, in contrast to the even curve of the thin outer lip. The shells are reddish horn with regular flammules or equivalent rows of minute squarish dots of red in the ground color. The broad columella is whitish. Embryonic shells of 3 whorls are globular, smooth except for growth lines, and even at this early stage possess a heavy, callused, but not flattened columella. (See pl. 11, fig. 18.)

The holotype of *F. laddi* (USNM 597433) and a number of paratypes (USNM 532559) were collected from rocks in a swift stream, the Lami River, on Viti Levu, Fiji Islands, May 30, 1926, by Dr. H. S. Ladd of the U. S. Geological Survey.

The holotype of *laddi* has 3 whorls remaining, and measures as follows: Height, 9.2 mm.; diameter, 8.2 mm.; aperture height, 8.0 mm.; aperture diameter, 5.8 mm. The flat, white columella is 1.5 mm. wide.

Comparison of all available figures and specimens has shown that there is only one described species of *Fijidoma.* It has been recorded to date from the upstream, swiftly flowing waters of the Rewa River and Lami River systems on Vit Levu.

Hubendick (1952) has rather completely described and figured the critical and diagnostic anatomy of animals of this genus. His slight misinterpretations of the reproductive anatomy are easily understood by anyone who has personally examined the gross reproductive anatomy of thousands of individual mollusks belonging to the "Melanian complex," including hundreds of individuals belonging to the family Thiaridae. Nearly all the biological peculiarities seen by Hubendick in the seven females of *Fijidoma maculata* available to him are the distinguishing biological characters possessed by every individual of the families Planaxidae and Thiaridae (Thorson, 1940, and Morrison, 1952). The assumption by Hubendick that these animals ever possess a testis must be histologically proven in order to refute the observed parthenogenicity of these females. Abbott (1952, p. 92) could not find sperm in living material or in histological sections of the gonads of six mature adults of the related *Tarebia granifera* (Lamarck). Hubendick did not recognize the completely separate, secondary or adventitious nature of the brood pouch of these animals. His "uterus" is not a part of the primary gonoduct as is the case in the Viviparidae and the Lavigeriinae, hence should not be called a uterus. Abbott (1952, p. 92) has pointed out that the brood pouch of the Thiaridae is not developed until the animal begins to reach maturity.

Hubendick's correction of the taxonomic placement of *Fijidoma* was incomplete; his references to its close relationship with the genus *Emmericia* of the family Hydrobiidae were erroneous. Elsewhere (Morrison 1949, p. 14) I have put on record the critical and diagnostic (male) reproductive characters of the subfamilies of the Hydrobiidae, including *Emmericia* of the Emmericiinae.

Family Thiaridae (in Africa)

Genus *Thiara* Röding, 1798

This typical genus of the family occurs in the east Africa region as well as in Asiatic waters.

Genus *Melanoides* Olivier, 1804

The genotype of *Melanoides* (Olivier, 1804, p. 40), *M. tuberculata* (Müller) 1776, was probably the first member of the family to be proved ovoviviparous in the thiarid fashion. Raymond (1852) described the brood pouch very well. His tales of the young going back into the brood pouch at night, however, must be completely discounted. What he did not realize was that there is only a partial release of the young at any one time, so that every time he looked into the brood pouch of an adult he found young still there—not back there again.

As mentioned above in the discussion of the genus *Potadoma*, all species of *Melanoides* are ovoviviparous and parthenogenetic. They must also agree with the genotype in the paucispiral character of the operculum. The species that differ from this pattern and are incorrectly placed in the genus must be placed elsewhere when their anatomic characters become known.

Genus *Tanganyicia* Crosse, 1881

Genotype: (*Lithoglyphus rufofilosus* E. A. Smith=) *Tanganyicia rufofilosa* (E. A. Smith) 1880.

With a shell similar to that of the American genus *Cubaedomus*, *Tanganyicia* from the shores of Lake Tanganyika differs most notably in possessing an operculum that is secondarily concentric around a paucispiral center. This African genus *Tanganyicia* (Crosse, 1881, p. 123) has a brood pouch similar if not identical in origin to that of all other known genera of the family Thiaridae. The species *rufofilosa* (E. A. Smith 1880, p. 426) has been anatomically described by Moore (1898c, p. 457). The primary reproductive organs are identical in their simplicity. The genital groove from the oviduct opening to the opening of the brood pouch is of exactly the same type (structurally demarcated) as that observed by me in the genus *Brotia*. The brood-pouch pore is on the right side, as in all the other genera. Moore (1898c, fig. 3), in his "semidiagrammatic representation," depicts the brood pouch passing under the oesophageal canal. The extensively developed brood pouches of many genera of this family may effectively almost surround the pharyngeal or buccal mass, but I believe the brood pouch is ordinarily dorsal thereto. Even if the brood pouch proves upon complete reexamination only to be beneath and expanded to the left of the buccal mass, these differences in the subhaemocoelic extent of an identically originating invagination can only be further proof of the distinction of the genus *Tanganyicia* from the other members of the family.

Moore (1898b, p. 307) listed *Tanganyicia* as a member of the Planaxidae, and again (1898c, p. 456) stated that *rufofilosa*, in the characters of the radula and alimentary canal, approximates the Planaxidae. This statement constitutes unbiased corroboration of the present studies which show that the Thiaridae and the Planaxidae are relatives from the same stock, since Moore was completely unaware of the identical type of reproductive characters possessed by the Planaxidae (see Thorson, 1940).

The statement of Moore that the genital groove is present "in both sexes" may be easily explained by the assumption that he had before him nongravid females and gravid females at the beginning of a seasonal reproductive period. He mentions only eggs in

the brood pouch, so his material must have been collected at the beginning of the brood-pouch nursing period for the species.

Genus *Stanleya* Bourguignat, 1885

Genotype: Stanleya neritinoides (E. A. Smith) 1880.

The figures of this shell look suspiciously like a variant of the genus *Tanganyicia*. The opercular and the animal characters must be discovered and compared in order to maintain the separation of *Stanleya*.

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